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GREATER PRAIRIE-CHICKEN ATTENDANCE AT LEKS AND STABILITY OF LEKS IN COLORADO

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ABSTRACT.—Greater Prairie-Chicken (*Tympanuchus cupido*) lek visitation and stability were examined in 1986–1991 on a 301-km² area in northeastern Colorado. Although 39–47 leks were active during any given year, about 23% of leks disappeared between consecutive years. Twenty of 80 leks were active all six years and 26 leks were active only one year. Relatively stable leks appeared to have greater male visitation than unstable leks. In addition, numbers of males visiting stable leks tended to be correlated with density of leks on the study area. Twenty-one radio-marked males were observed on 286 occasions during peak display periods; 95.1% of those observations were on lek sites. Rates of lek visitation were similar for adults and yearlings captured on leks or during winter. *Received 3 June 1991, accepted 20 Oct. 1991.*

Many species of Tetraoninae congregate on leks for breeding including Sage Grouse (*Centrocercus urophasianus*), Sharp-tailed Grouse (*Tympanuchus phasianellus*), Lesser Prairie-Chicken (*T. pallidicinctus*), and Greater Prairie-Chicken (*T. cupido*). Density of leks and attendance of males at leks have been used as indices of abundance of Greater Prairie-Chicken populations at many locations (e.g., Hamerstrom and Hamerstrom 1973, Horak 1985, Kobriger et al. 1988). Despite use of such indices, little is known about male attendance at leks and the stability and/or distribution of leks (Cannon and Knopf 1981).

Robel (1970) suggested that about 50% of male Greater Prairie-Chickens observed prior to the breeding season occupied territories on leks during the peak of the breeding season; presumably non-territorial males were in adjacent areas (Ballard and Robel 1974). Similarly, Rippin and Boag (1974) suggested that some male Sharp-tailed Grouse were non-territorial in areas adjacent to leks, while waiting for territories on leks to become available. However, actual locations of these 'surplus' males are difficult to determine; they may either be in areas adjacent to leks or on other leks.

Numbers of male Greater Prairie-Chickens at leks in Kansas declined throughout the breeding season (Robel 1970). In contrast, numbers of males remained relatively stable at leks in Wisconsin (Hamerstrom and Hamerstrom 1973). It is not known whether changes in lek visitation are influenced by mortality of males during the breeding season and/or changes in the likelihood of males to visit leks.

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Adult males may form a stable territorial population while non-territorial males may be responsible for observed fluctuations in attendance of males at leks; these differences in attendance may be related to differences between "permanent" (referred to as ancestral leks by Hamerstrom and Hamerstrom [1973]) and "temporary" (referred to as "satellite" leks by Hamerstrom and Hamerstrom [1973] and "adjunct" leks by Grange [1948]). Whereas permanent leks may be active every year, temporary leks may appear and disappear during years of population fluctuations (Grange 1948, Cannon and Knopf 1981).

Counts of both leks and males have been used as indices of status of prairie grouse populations. Consequently, the objective of this research was to document the attendance of males at leks and the stability of leks in a population of Greater Prairie-Chickens. Because stability of leks may be closely related to attendance of males at leks, we examined (1) stability of leks, (2) relationships between male attendance at leks and lek stability and density, and (3) frequency of occurrence of radio-marked male Greater Prairie-Chickens at leks.

METHODS

We inventoried a 301-km^2 area 10 km northeast of Eckley, Colorado (40°11′N, 102°22′W), each year from 1986 to 1991 to estimate lek density and attendance of male Greater Prairie-Chickens (after Hamerstrom and Hamerstrom 1973). The habitat was primarily gently rolling rangeland consisting of grassland, sand sagebrush (*Artemisia filifolia*), and small soapweed (*Yucca glauca*) intermixed with irrigated cropland, primarily corn. In general, habitat on the area studied remained consistent throughout the 1986–1991 period (Schroeder and Braun 1992).

Two or more displaying males in a cluster were considered a lek. Different leks generally were separated by at least 0.5 km (or distinct topography). We conducted two complete surveys of the area each year. Attendance for each lek (within a year) was estimated using the maximum of at least two counts of males at each site. Although males on all leks were flushed and counted, leks were approached slowly in order to determine if females were present. Males at leks were counted during March and April, peak periods of male attendance at leks (Hamerstrom and Hamerstrom 1973).

Trapping was concentrated on a core area of approximately 100 km^2 during 1986–1988. Male Greater Prairie-Chickens were captured on leks, using walk-in traps (Schroeder and Braun 1991) and cannon nets, and at winter feeding sites using walk-in traps baited with corn. Thirteen adults and nine yearlings were captured on leks and seven adults and five yearlings were captured during winter. Captured males were banded with a numbered aluminum band and a unique combination of three colored plastic bands and fitted with battery- or solar-powered radio transmitters attached to poncho-type markers (Amstrup 1980). Radios weighed 1.8–2.3% of each bird's body weight. Birds were classified as yearlings (first breeding year) or adults (>first breeding year) (Ammann 1944).

Observations of radio-marked males were made between 0.5 hours before to 2.0 h after sunrise during 1 March–30 April 1986–1988; these dates were chosen to represent the normal display season for males of 15 February–15 May. Radio-marked Greater Prairie-Chickens were located by using a portable Telonics' receiver and three-element Yagi antenna. Ob-

servations consisted of visual sightings of radio-marked males on leks (usually from 0.2 to 1.0 km away) and/or triangulation (3 or more azimuths obtained ≤0.5 km of target transmitters and at angles-of-incidence >35° and <145°). Approximately 40% of the observations were obtained visually. All locations were recorded as Universal Transverse Mercator coordinates (nearest 10-m interval).

Examinations of accuracy indicated that 90% of the locations derived by triangulation were within 250 m of actual locations (Schroeder 1991). If an estimated location was within 250 m of the center of a lek, the radio-marked bird was assumed to be on the lek. There are three basic reasons why we believe these results were accurate. First, triangulation accuracy for radio-marked males was probably better than the 250-m estimate generated for radios in known locations such as nest and mortality sites (Schroeder 1991); distances between observers and radio-marked males were closer and males were in prominent locations. Second, since leks may be >250 m in diameter, these results were considered conservative. Third, radio telemetry was used to estimate locations of radio-marked males before leks were approached (when traps were checked); males estimated to be on the lek flushed with the other males on the lek.

RESULTS

Lek stability.—Eighty leks were documented on the study area during 1986–1991 (Fig. 1); single males displayed at an additional 11 locations. The number of leks ranged between 39 in 1991 and 47 in 1988. The density of leks was relatively stable at 0.14 leks/km^2 (Table 1). Numerous leks disappeared between consecutive years; eight of 41 between 1986 and 1987, 12 of 42 between 1987 and 1988, 13 of 47 between 1988 and 1989, eight of 42 between 1989 and 1990, and eight of 41 between 1990 and 1991. The average annual disappearance rate for leks was 22.9%. Twenty leks were active all six years, six for five years, seven for four years, six for three years, 15 for two years, and 26 for one year. The relatively large numbers of leks active either six years or only one year appeared to reflect a bimodal tendency in stability of leks.

Numbers of males visiting leks ranged between two and 28; density of males observed on the study area ranged between 0.98 in 1986 and 1.69 males/km^2 in 1988 (Table 1). Male attendance at individual leks was positively correlated with their stability ($r = 0.438$, $P < 0.001$, N = 252 [pooled sample]). Average attendance of males was 3.62 (SD = 1.77) at leks active one year, 6.67 (SD = 5.29) at leks active two years, 7.78 (SD = 5.06) at leks active three years, 8.57 (SD = 3.76) at leks active four years, 7.17 (SD = 3.32) at leks active five years, and 10.84 (SD = 4.90) at leks active all six years (Fig. 2).

Although total attendance of males at leks fluctuated between years, fluctuations apparently were not in response to density of leks on the study area ($r = 0.423$, $P = 0.403$). Despite small sample sizes, male attendance at relatively stable leks tended to be positively correlated with number of leks on the study area; $r = 0.713$ ($P = 0.112$) for leks active six years,

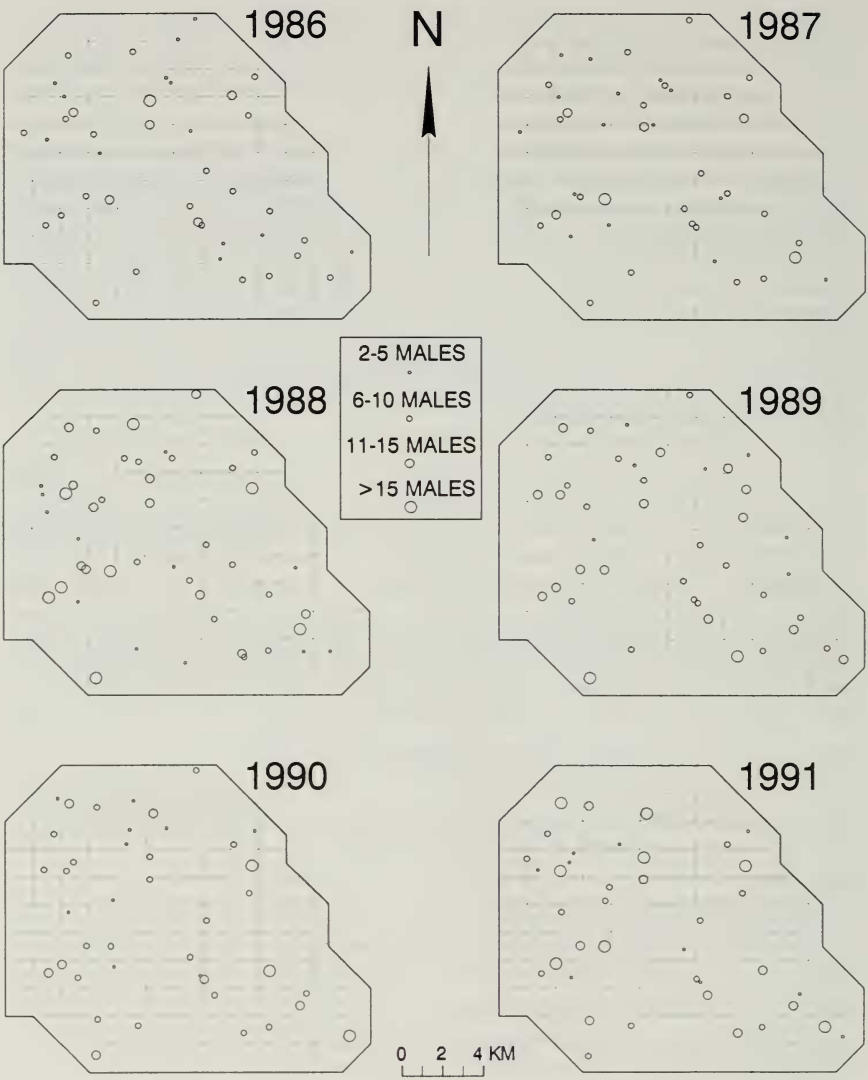

FIG. 1. Distribution of Greater Prairie-Chicken leks on a 301-km² study area in northeastern Colorado, 1986–1991. Each square represents one cadastral section (2.59 km²).

$r = 0.811$ ($P = 0.050$) for leks active five years, $r = -0.346$ ($P = 0.502$) for leks active four years, $r = 0.848$ ($P = 0.033$) for leks active three years, $r = 0.158$ ($P = 0.765$) for leks active two years, $r = 0.531$ ($P = 0.278$) for leks active one year.

Attendance of males on leks.—The average date for the maximum count

TABLE 1
INDICES OF LEK STABILITY AND ABUNDANCE OF MALE GREATER PRAIRIE-CHICKENS ON A 301-KM² STUDY AREA IN NORTHEASTERN COLORADO, 1986–1991

Index	1986	1987	1988	1989	1990	1991
Number of leks						
Active	41	42	47	42	41	39
Additional (not previously active)	—	9	15	6	5	4
Active during previous year	—	33	30	34	34	33
Disappearing during previous year	—	8	12	13	8	8
Lek density (leks/km²)	0.14	0.14	0.15	0.14	0.14	0.13
Number displaying males/lek						
$\bar{x}$	7.22	7.29	10.47	8.86	8.41	9.74
SD	3.89	4.39	5.97	3.86	4.72	5.80
Male density[a] (males/km²)	0.98	1.02	1.69	1.23	1.17	1.08

[a] Includes males displaying alone.

of males on leks was 1 April (SD = 3 days). However, examination of male attendance throughout the breeding season (late Feb–early June) indicated that attendance was relatively stable during March and April, particularly on undisturbed leks (those which were not used for trapping during the breeding season) (Fig. 3). Regardless of disturbance status, attendance appeared to decline after April.

Annual changes in attendance of males at leks may reflect either regional or local changes in lek visitation (Fig. 1). Regional changes would be characterized by a positive correlation between changes in annual attendance of males at neighboring leks (if the number of males/lek increases, the number of males/lek on the nearest neighboring lek should also increase). In contrast, local changes or "shifts" in lek visitation would be characterized by a negative correlation (if number of males/lek increases, number of males/lek on the nearest neighboring leks should decrease). Although changes were not correlated for 1986–1987 ($r = 0.062$, $P = 0.663$), 1987–1988 ($r = -0.069$, $P = 0.582$), and 1988–1989 ($r = -0.035$, $P = 0.791$), they were negatively correlated for 1989–1990 ($r = -0.230$, $P = 0.028$) and 1990–1991 ($r = -0.695$, $P < 0.001$). The relationship was not significant ($r = -0.076$, $P = 0.184$) for all years combined.

Frequency of occurrence of radio-marked males on leks.—Of 34 male Greater Prairie-Chickens fitted with radio transmitters, 13 could not be observed during the breeding season (10 died and three had radios removed). Of the remaining 21 males, 13 males with a minimum of nine

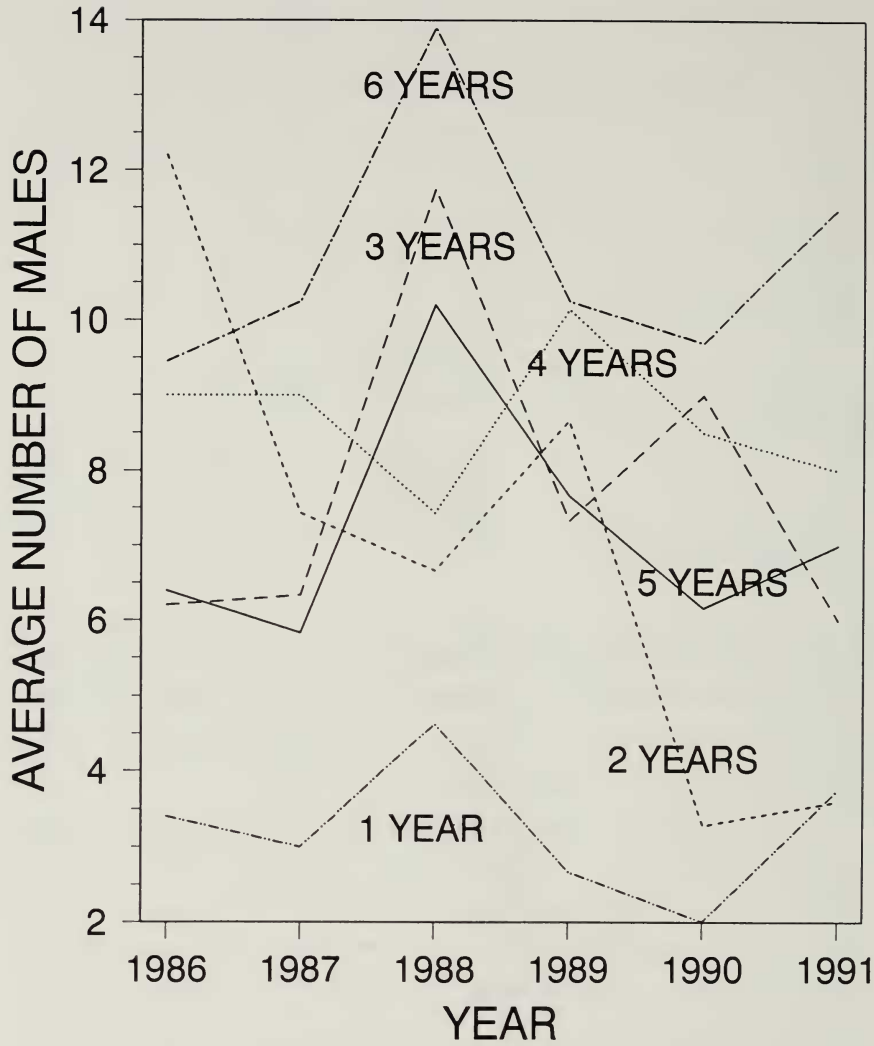

FIG. 2. Attendance of male Greater Prairie-Chickens at leks in northeastern Colorado, 1986–1991, in relation to the lek's stability (active for 1 to 6 years).

observations during normal display periods ($\bar{x}$ = 20.5 observations/bird [SD = 11.5, range 9–37]) were on leks an average of 94.5% (range 86.7–100%) of the time (each bird weighted equally). There was no correlation between number of observations/bird and the frequency of occurrence of males at leks ($r = 0.079$, $P = 0.797$). Although five males captured during

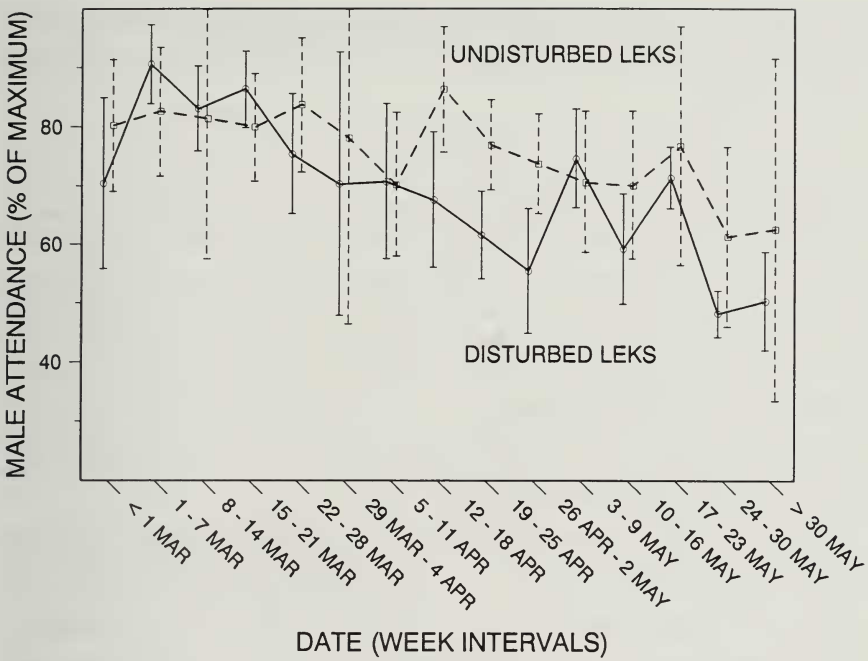

FIG. 3. Average weekly attendance (% of maximum attendance) of male Greater Prairie-Chickens on 28 undisturbed (not used for trapping) and 12 disturbed (used for trapping) leks on a 301-km^2 study area in northeastern Colorado, 1986–1991. Only leks with >2 counts within a breeding season were used in the analysis.

winter had slightly higher lek attendance rates than eight males captured on leks ($\bar{x}$ = 96.8 vs 93.1%), differences in rates of lek attendance by individual males were not detected (χ^2 = 10.647, df = 12, P = 0.559).

When lek attendance of radio-marked males was examined independent of individual differences, the frequency of occurrence of males at leks was 95.1% for 286 observations of 21 males (including eight males with less than 9 observations). Males captured during winter had slightly higher (χ^2 = 2.719, P = 0.099) frequencies of occurrence on leks than males captured on leks (96.9% vs 92.7%).

Although there were no apparent differences in lek visitation associated with age (t = 0.910, P = 0.382), yearlings visited more leks during the breeding season than adults. Three of four yearling males visited more than one lek, while only one of 17 adults visited more than one lek (χ^2 = 10.032, P = 0.002). In addition, one yearling was observed on four leks, while another was observed on six leks. The latter male also was

observed on two leks in the same morning. In only one case was a radio-marked yearling male not observed on a lek during the normal morning display period.

DISCUSSION

Leks differ with respect to stability, and permanent leks may be more desirable for territory acquisition than temporary leks. For example, Lewis and Zwickel (1980, 1981) determined that non-territorial yearling male Blue Grouse (*Dendragapus obscurus*) spent more time near permanent territories. Although there was no specific evidence of age composition of male Greater Prairie-Chickens at temporary leks, it was possible they were generally comprised of males unable to obtain territories on permanent leks (Cannon and Knopf 1981). Presumably these birds were more likely to be yearlings. Older males were more likely than young males to occupy territories on leks in Kansas (Robel 1970, Robel et al. 1970, Ballard and Robel 1974, Robel and Ballard 1974).

Yearling Greater Prairie-Chickens were observed visiting more leks than adults (at least six leks by one yearling male). Although multiple lek visitations have been reported in other populations, ages of males were rarely known (Silvy 1968, Arthaud 1970, Robel et al. 1970, Hamerstrom and Hamerstrom 1973, Robel and Ballard 1974). Removal of dominant males increased male-male interactions/morning/bird from 4.5 to 11.0, perhaps because of an influx of lower-status males (usually younger birds) onto vacant territories (Ballard and Robel 1974, Robel and Ballard 1974). Rippin and Boag (1974) found that removal of territorial male Sharp-tailed Grouse from leks resulted in an influx of new males; they suggested that newly established males were more likely yearlings that had previously been non-territorial in areas associated with the lek.

Movement of males among different leks, particularly young and/or non-territorial males, may explain why an average of about 80% of the maximum number of males were observed on leks during March and April (67% for leks active one to three years and 83% for leks active more than three years). Consequently, as the number of counts of males on a lek increases, the maximum number of males counted is also likely to increase. Although this consideration probably did not influence the results of this study (survey intensity was similar in each year), this consideration should be addressed in all studies.

There are numerous possible explanations for variability in stability of leks including (1) formation of smaller temporary leks near larger permanent leks, (2) differences in recruitment rates of males at permanent and temporary leks, (3) local and regional fluctuations in abundance of males, (4) compensatory changes in abundance of males at neighboring

leks (if one lek increases, an adjacent lek may decline), (5) movement of leks, (6) habitat changes, and/or (7) changes in location of nesting habitat for females.

Correlations in annual changes of male attendance at neighboring leks appeared to be either non-significant or negative, indicating that fluctuations in lek visitation may be caused by local, rather than regional, changes or "shifts" in abundance of males. These results were supported by anecdotal observations of shifts in actual lek locations. For example, in 1987 fire burned an area 0.5 km from one lek that was active for at least four preceding years (1984–1987). In the first spring following the fire (1988), several males were displaying on a new lek site within the boundaries of the burned area, while a few males remained on the old lek site. Only the new "burned" site was used in 1989–1991. In another example, a new lek formed on a newly disturbed site in 1990; the new lek was in the middle of, and relatively close to, three lek sites that had been occupied continuously since 1984 (in one case, the lek site was occupied as early as about 1910). The average combined attendance at the three "old" leks was 18 during 1986–1989, four in 1990, and zero in 1991; the new lek had 14 males in 1990 and 18 in 1991.

Several researchers have suggested there is a relationship between location of nesting habitat and lek locations; each lek may have its own population of females that breed at, and subsequently nest near, the lek (Westemeier 1972, Sanderson et al. 1973). Consequently, permanent leks may be in areas with 'better' nesting habitat. However, nests tended to be farther from the nearest lek than random locations in Colorado; distances between nests and the nearest lek were 0.23–2.39 km ($\bar{x}$ = 1.01 km) for 81 nests (Schroeder 1991). In addition, there was a positive correlation between number of males/lek and nest-lek distance ($r = 0.320$, $P = 0.001$).

Variation in lek attendance may be due to time of year (Bradbury et al. 1989), weather (Hamerstrom and Hamerstrom 1973), or overall status of the population. Visitation rates of Sage Grouse were > 90% during the period of peak male attendance at leks and between 67% (yearlings) and 100% (adults) during the peak of hen attendance (Emmons and Braun 1984). We found that lek visitation by Greater Prairie-Chickens in northeastern Colorado remained relatively constant at 95% throughout March and April.

Although northeastern Colorado is on the western edge of the Greater Prairie-Chicken distribution in North America, comparison of this population with those in other regions indicates they are comparable with respect to both density of leks and number of males/lek (Kansas [Horak 1985], Missouri [Christisen 1985], Nebraska [Kobriger 1965], North Da-

kota [Kobriger et al. 1988], and Wisconsin [Hamerstrom and Hamerstrom 1973]). Furthermore, brief lek searches on a 631-km^2 area surrounding the main 301-km^2 study area in northeastern Colorado during May 1988 resulted in detection of an additional 40 display sites. The abundance of leks in areas adjacent to the area intensively studied in northeastern Colorado indicates that this population was not on the "edge" of occupied range.

These results for male lek attendance pertain to serious issues concerning estimates of population size of Greater Prairie-Chickens and other prairie grouse. Counts of males are frequently used to estimate trend and size of populations of prairie grouse. Robel's (1970) paper has been cited as evidence that the actual number of males may be twice as high as the number counted on leks (Hoag and Braun 1990, Van Sant and Braun 1990). However, the data in this study indicated that most males (about 95%), may be attending leks every day. Thus, population size could be over-estimated if lek attendance rates of 50% are used.

In addition to lek visitation, methods of surveying lek attendance of prairie grouse should be evaluated. Accurate counts of males may be easier to obtain when birds are flushed than when observed from a distance. Some males may be on the edge of leks and, hence, difficult to observe. Additionally, permanent leks may be more consistent with respect to male attendance than temporary leks. Differences in attendance may be important if permanent leks are easier to find than temporary leks. This latter consideration could affect estimates of both lek density and male attendance (Cannon and Knopf 1981). The methodology for estimating numbers of males could be of critical importance if counts of males are used to estimate population size. Counts of male Greater Prairie-Chickens should be made only during the 1 March–30 April interval and preferably during the peak of hen visitation if estimates of male population size are desired.

If lek densities and/or counts of males are to be used for monitoring the status of populations, their respective disadvantages and advantages should be addressed. Although lek densities have been suggested to provide a better indication of a population's status (Cannon and Knopf 1981), lek densities may be difficult to estimate accurately. For example, conclusions might vary dramatically if some leks are not found. Similarly, estimates of lek numbers are rarely if ever obtained with a corresponding estimate of precision. Hence, the validity of the lek numbers is difficult to support. In contrast to lek density, numbers of males may be relatively easy to obtain and justify with estimates of precision. Although Cannon and Knopf (1981) suggested that numbers of males were not as accurate as counts of leks for evaluating the status of populations, understanding

the differences in male attendance associated with the stability of the leks may help improve the prospects for using counts of males.

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